THE ROLE OF ORGANISMS IN THE EARLY STAGES OF SOIL FORMATION

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PERHAPS the nearest thing to soil, as we think of it, that is formed in the absence of life is a mass of rock particles weathered above the limit of life on a mountain, and collected by erosion in a depression. Heat and frost, the kinetic and chemical energy of the rain and the force of gravitation have made this mass of rock particles from which life could produce soil. But as weathering and deposition proceed, the mass of particles tends to become a less rather than a more suitable potential habitat for living organisms. Gravitation causes the particles to compact into the smallest available space, leaving no room for air and water. All the energy, chemical and physical, received by the system is immediately dissipated in the form of heat. There is no mechanism or organization in the system for storing energy. If rain falls on it, mineral plant nutrients, released from the weathering rock, tend to be washed out and lost. If rock weathering goes on long enough, a stage will ultimately be reached when no plant nutrients are left and no plants can grow.

The appearance of plant life on the rock particles transforms the site into a system which can absorb and store radiant energy. We can observe the first stage—even preceding the comminution of rock by physical weathering—of the making of soil in the colonization of bare rocks with lichens, which are symbiotic associations of algae and fungi. Lichens can photosynthesize, and thus store solar energy for subsequent use by insects and microorganisms which feed on the living and dead lichens. Lichens also penetrate the surface layers of the rock and cause them to crumble. They dissolve mineral substances from the rock and absorb them into their tissues. When these tissues die and decompose, both the photosynthesized organic matter and the absorbed minerals will fall back onto, and mingle with, the crumbling rock surface. A primitive soil will have been created which will be an improved habitat not only for lichens and their accompanying predator insects and microorganisms, but for other predators on, and symbionts with, these.

The growth of lichens and the etching of a rock surface by them can

be observed on almost any rock. Sometimes, in hollows, it is possible to observe the accumulation of primitive soil consisting of flakes and particles severed from the rock by lichens and mingled with organic remains. These 'organo-mineral' particles may be the first manifestation of that unique and most characteristic feature of soil formation, the chemical union of complex organic and complex mineral compounds. They are the relatively simple prototypes of the 'humus–clay complexes' of more fully developed soils.

Polynov (1945) was one of the first to draw attention to the significance of 'organic weathering'. He maintained that the finer particles of mineral soils could not be produced by purely mechanical and inorganic weathering, and that in the absence of living organisms these processes would long since have removed most of the unstable minerals, including available nutrients, from the earth's crust. He believed that organic weathering by the action of microorganisms was occurring even in a desert.

In recent years numerous studies have been made by Russian scientists of the earliest stages of soil formation from massive crystalline rocks. The object was to study the effect of pioneer organisms, especially lichens and mosses, on the decomposition of rock. Unweathered rock at high altitudes was selected in order to avoid complications that would have been introduced by the presence of already weathered material and of higher forms of life.

These studies showed that lichens and mosses can extract nutrients (P, Mg, Ca, K, S, Fe) from rock that are unavailable to higher plants and return them to the 'soil' in a more available form. When sufficient soil—the mixture of rock dust and lichen residues—had collected, mosses replaced lichens, and when the accumulations were sufficiently deep, alpine grasses appeared. Microorganisms, including bacteria, fungi, algae and actinomycetes, occurred on both bare and covered rocks. These organisms would certainly take part in the decomposition of organic residues, and there was evidence in the coloration and configuration of the rock surfaces that they also took part in biochemical weathering and affected the chemical and mineralogical composition of the weathered material. Among the most active weathering agents were green and blue-green algae and diatoms, and the products of weathering included amorphous silica and common soil minerals such as montmorillonite and beidellite. At the stage of soil development when grass appeared, about 30 per cent of the minerals present were new products, some apparently synthesized in the tissues of the vegetation. Many of these minerals were of the montmorillonite type, with magnesium replacing aluminium in the crystal lattice.

The lichen population varied with the nature of the rock. Thus *Parmelia* was very common on acid rocks, *Acarospora* and *Lecanora* on limestones. Lichens were especially active in breaking down limestones and in producing exchangeable calcium in their dust which in one case (Aidinyan, 1949) had an exchange capacity of 10–50 m.e./100 g and was 60–80 per cent saturated with Ca. The fact that the silica–sesquioxide ratios of the colloid fraction and of the lichen ash were identical (1·3) and about half that of the original rock was evidence of a biological origin of the colloids.

Polynov constructed 'series of biological absorption' according to which the first lithophile organisms (lichens) absorbed predominantly P (and possibly S) from rock; later organisms absorbed Ca, Mg and K, then Na, Fe and Si, and finally Al. Other Russian workers have observed the early activation (if that is the word) of phosphate by the first settlers on bare rock. Thus the embryonic soil accumulates by biological action all the mineral elements required for at least the lower forms of plant life. The iron, aluminium and silica accumulate in the organo-mineral complex and may form colloidal clay minerals when the organic matter decomposes. There is not much aluminium available for the production of aluminosilicates, and it is suggested that magnesium, which appears in the fine earth of lichen dust in non-exchangeable form, may replace aluminium in the crystal lattice.

Schatz (1963) showed that lichens do their weathering at least partly by chelation, and pointed out that they excrete greater amounts and more kinds of chelating agents (lichen acids) than other plants.

A few studies have been made of the microflora accompanying lichens in primitive soils. Krasilnikov (1949) found microfloras of 5–50 million, mainly bacteria with some algae and fungi, per gramme of soil. The bacteria were mainly autotrophs and could be regarded as accumulators of carbon from the air. Azotobacter was absent, which may indicate that the first organisms get their nitrogen from the rain and build it up into the organic cycle. Glazovskaya (1950) found green and blue-green algae and diatoms on both bare and lichen-covered mountain rocks; some of these might be nitrogen-fixing. She stated that they also synthesized aluminosilicates of the montmorillonite type.

Webley *et al.* (1963) investigated quantitatively the microflora of rocks covered with varying densities of lichen cover. Bacteria and fungi accounted for most of the organisms, with a few actinomycetes. In general, numbers of microorganisms increased with increasing degree of colonization, and by far the largest numbers were found in what the authors call 'raw soil', found in rock crevices and rich in organic matter. Several bacterial species (which were not determined)

were able to render silicates soluble when tested in pure culture. Penicillia were often the dominant species of fungi, and Müller and Förster (1963) have recently shown that these fungi, in nutrient cultures, release potash from minerals like felspar and orthoclase. Henderson and Duff (1963) report experiments showing that, at least in cultures, some fungi can break down rock minerals into metal and silicate ions.

Several Russian workers have commented on the high humus content of primitive soils, though I have not found any actual figures. Stebaev (1963) observed almost complete inactivity of ammonifying bacteria in lichen- and moss-covered primitive soils; so it may be that in the early stages humus and nitrogen are conserved while they are in short supply. He and other Russians (e.g. Evdokimova, 1957) state that lichens provide a habitat for a group of oligonitrophile micro-organisms involved in the nitrogen cycle on primitive soils.

Thus lichens perform many simple acts of soil formation. They break down solid rock physically and chemically, absorb from the rock nutrient elements that would otherwise remain unavailable, synthesize secondary clay minerals and produce a sort of clay–humus complex. Thus they have considerable power to modify the environment in a way that makes it more suitable for living things—in other words, to create a habitat in which more life forms can exist. Neither fungi nor algae, nor both living independently, can do all these things, though some, especially blue-green, algae seem able to decompose minerals and bring silica, iron and aluminium into solution. According to Polynov, algae appear before fungi in the lichen symbiosis. The lichen symbiosis may be regarded as the first cooperative enterprise between organisms in making soil. And most of soil formation consists of the results of cooperation or antagonism between organisms, but the processes get so complicated as their number and variety increase that they are mostly beyond our present comprehension. But this initial cooperative enterprise between fungi and algae is something we can see the results of and understand.

According to the Russian workers, the next stage in soil development from bare rock is the substitution of lichens by mosses. This happens when a few millimetres of lichen dust have accumulated, either in place or by deposition. Polynov opined that the very first stages of biological soil formation are effected by plants—as one might expect, since the main role of animals in soil formation is to transform the radiant energy collected by plants—and animals become active agents when there is sufficient plant and mineral material available for them to multiply. There is a micro-arthropod population at the lichen stages of soil development that increases rapidly when lichens

give way to mosses. The first mosses (Polynov mentions *Hedwigia ciliata*) penetrate and break up the solid rock, their successors (of the *Hypnum* type) do not do much rock smashing, but form a layer of raw humus which in time produces an illuvial humus horizon below the surface.

Stebaev (1963) has recently published a detailed paper on the microfauna of primitive soils, starting from bare rock through successions of lichen- and moss-covered soils. He found that the species composition of the fauna was almost unaffected by the nature of the rock and the plant association, and depended on the age of the soil and the microclimate. The main groups found were acarids, oribatids, Collembola and Insecta; starting from the most primitive soils, they developed in that order. Mesofauna—insects, oligochaets, myriapods—were almost absent until the moss stage was reached, when they increased rapidly. The function of these primary animals in the soil-forming process seems to be to produce humus for the mosses and lichens. Stebaev emphasizes the near-absence of ammonifying bacteria, which suggests that conditions are favourable for the conservation and building-up of the supply of soil nitrogen.

At a later stage, the moss-covered soils are invaded by grasses, and then the first signs of an aggregate structure become apparent—at first around the roots of single grass plants and finally throughout the soil (Parfenova, 1950). Plant roots are the first agents in making a soil structure—and I cannot overstress my belief that structure should be studied as a biological rather than as a physico-chemical phenomenon. Structure is the ultimate expression of the activity of all the soil organisms in making a habitat for themselves, that is, of the whole, or most, of soil ecology. The development of a structure is itself a symptom of the intensifying struggle for existence and of the selection of the components of the soil population by the whole population.

As we have seen, when rooting grasses colonize primitive soils, signs of aggregate formation appear. Aggregate formation itself improves the habitat for insects and other small animals which begin to multiply rapidly. According to Stebaev, there is quite an abrupt change in the proportions of microfauna and mesofauna as one passes from lichen- and moss-covered to plant-covered soils; the mesofauna now greatly exceeds the microfauna in mass, if not in numbers. At this stage conditions are ripe for the formation of true humus products by the digestion and excretion of plant residues by the soil fauna.

Barratt (1962) found that much of the organic matter in recently colonized coastal sand dunes consisted of faecal pellets of mites and Collembola, the pioneer fauna of the dunes. This excrement is in the form of a colloidal gum which can be used to stick particles

together. But it will not be used to much effect unless there is some agent to use it. Barratt noticed that fungal hyphae were active agents in the dunes in binding sand particles into primitive aggregates. In older dunes, supporting a gorse cover, distinct L, F and H horizons had appeared in a sandy mat showing marked aggregation by fungal hyphae and faeces. Bond (1960), working with Australian sands, also noticed that many sand grains were held together by fine fungal filaments and that the binding action persisted after quite strong mechanical treatment. Examination of other soils revealed that small aggregates (< 2 mm) from most surface horizons contained similar but finer filaments, forming a strong network within the soil crumbs.

Many other workers have noticed the binding effects of fungal filaments on soil particles, mainly in mature soils. Feeding glucose to soil results in a vigorous multiplication of fungi and bacteria, and an increase in aggregation is sometimes observed, associated with an increased development of fungal hyphae (McCalla and Haskins, 1961; Iimura and Egawa, 1956).

As regards the effect of pioneer organisms on the plant-nutrient content of soil, algae, fungi and possibly some actinomycetes and bacteria seem capable of releasing nutrients from solid rock, thus preparing the ground for higher plants. These, of course, remove the available nutrients, and if they are slowly maturing perennials like trees, may cause a marked fall in fertility, measured chemically. It is known that some roots can get hold of nutrients unavailable to others, and it seems probable that pioneer plants that can survive under conditions of very low mineral availability will be those which can best utilize unweathered or slightly weathered minerals. Once absorbed by plants, the minerals, after passage through animals and microorganisms, will ultimately return to the soil in more available form.

Wright's (1956) studies on the Culbin sands showed that afforestation with pine and spruce markedly reduced the nutrient content until the canopy closed, when the loss by leaching and root absorption was balanced in the surface layer by return of nutrients in the leaf fall.

The closing of the canopy also increases the moisture reserves of the soil, not only by reducing evaporation but also by the formation of a moisture-holding litter horizon. This is a direct effect by organisms on the evolution of their habitat, the soil. Zonn (1963) states that when soil formation starts on a loose deposit (as distinct from solid rock), like a sand dune or fresh volcanic lava, water is often a limiting factor to plant growth, and deep-rooting plants such as trees

tend to come in early because they can get their water from beneath the surface and thus compete successfully with shallow-rooting plants. As the canopy closes, the soil atmosphere gets moister, and mosses appear which help in holding moisture in the topsoil. Thus one of the first acts of pioneer organisms in improving their habitat is to increase its water-holding capacity. Air capacity, except in very compact deposits, does not become a limiting factor to the survival of the edaphon (including roots) until water is retained in most of the pores, to the exclusion of air. The edaphon then has to get busy with creating a porous structure. The Russian workers claim that an aggregate structure begins to form in primitive soils when grasses succeed lichens and mosses. Perhaps when forest quickly occupies unformed soil, without a dense root mat on the surface, structure formation is done primarily by animals. At least we know that in this country earthworms play a leading part in maintaining a crumb structure and that in the absence of a rich fauna such a structure does not form in mature forest soils.

CONCLUSION

Starting with solid rock right at the beginning of soil formation, the principal function of organisms, particularly the algal–fungal symbioses of lichens, is to comminute and dissolve, that is, to weather the rock. When the parent material is an already weathered deposit, like a sand dune, a lava deposit or a spoil heap, organic weathering is not an absolute prerequisite of soil formation, but presumably it goes on all the same. Such deposits are already potential habitats for photosynthesizing and, therefore, energy-accumulating higher plants, provided their roots can penetrate the soil and find in it adequate nutrients, water and air. Roots spreading through the soil create a rhizosphere habitat in which a rich microflora can exist and consume living and dead root material, producing a habitat for a microfauna and later for a predatory mesofauna. All these pioneer animals and plants are concerned in a desperate struggle for existence in a harsh environment and, like human beings in comparable circumstances, spend most of their energy in trying to improve the habitat.

By the time trees have formed a canopy over, or grasses or heather have fixed, the drifting dunes, there are enough insects and other small animals to produce in the soil, with the help of bacteria, enough humus slime to enable fungal hyphae to bind the separate soil particles into aggregates. Aggregation increases porosity and thus enables larger animals to colonize the soil. In course of time, burrowing and

soil-eating animals will come in which, by pushing about and eating the soil, will cause profound and visible developments in its physical architecture and chemical composition. Plant roots, particularly those of grasses, do the same. The stage has now been reached, in studying the evolution of the soil habitat, at which the trained ecologist should take over from the abiotically-minded pedologist.

Summary—Soil formation is the process whereby organisms, using energy absorbed in photosynthesis, make and maintain a habitat. Starting from massive rocks, the early stages of soil formation involve organic weathering by lichens, mosses and microorganisms, resulting in solution of plant nutrients from the rock and in the formation of secondary clay minerals and an embryonic clay–humus complex. When grasses succeed mosses, an aggregate soil structure is produced, forming a habitat for a mesofauna which makes humus which can be used by e.g. fungal hyphae for further aggregation. On already weathered loose deposits, soil formation may start with colonization by higher plants, and an early role of the colonizing organisms is often to increase the moisture-holding capacity of the habitat.

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